

A neural field model for saccade planning in the Superior Colliculus: speed-accuracy tradeoff in the double-target paradigm

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Abstract

Recent experimental and theoretical studies suggest that the Superior Colliculus (SC) actively contributes to the integration of contextual information for the planning of saccadic eye movements. However, it is still under considerable discussion whether the neuronal processing mechanisms in the SC are also sufficient to account for target selection in response to multiple targets. Here we use a neural field model which captures the basic pattern of lateral interaction in the SC to elucidate the role of the SC for the timing and metrics of a saccade in a double-target paradigm. Our modeling results suggest a more active role of the SC also for target selection.

Key words: neural fields; saccade planning; Superior Colliculus; double-target paradigm

1 Introduction

Selecting one from many objects in the visual field and directing the gaze to it by a saccadic eye movement is a fundamental behavior of primates. The investigation of this behavior by means of the double-target paradigm reveals a speed-accuracy tradeoff for a certain range of spatial separations between the two targets [9, 4, 2]: (1) Saccades of long latency are directed to one of the

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targets (*target selection*). The distribution of saccadic endpoints is bimodal. (2) Short-latency saccades (including express saccades) land at an intermediate position between the targets (*target averaging*). In this case the endpoint distribution is unimodal.

It has been proposed that the slower target selection process is organized in the cortex, and that the SC as a fast, reflexive system is concerned with the planning of short-latency saccades [9]. Averaging saccades are assumed to result from the superposition of stimulus-induced activity on the collicular visuomotor map.

However, in the two pathway hypothesis it has been neglected that also saccades with short latencies may be target-directed whenever the spatial separation is large enough [9, 2]. Moreover, there is recent experimental evidence for strong inhibitory connections between different loci within the collicular saccade zone [7] which may be seen as a neural basis for a competition process. These findings let us speculate that the SC may be involved also in target selection. Within the theoretical framework of dynamic neural fields [1] we therefore address the question whether the known neuronal interaction mechanisms in the SC may be sufficient to explain the observed speed-accuracy tradeoff.

2 Model

Neural field models have been used in the past to discuss aspects of the planning of eye and arm movements such as the integration of different information sources or decision making in ambiguous stimulus situations [6, 10, 5]. The central feature of these field models is a pattern of recurrent interaction in which field locations are mutually excitatory over short distances and mutually inhibitory over larger distances. There is strong anatomical and physiological evidence for such an interaction scheme on the motor map of the SC [7]. Kopecz and Schöner showed for the saccadic double-target paradigm that neural field models can in principle capture the dependency of target averaging and selection on the spatial separation between targets [6]. More recently, Trappenberg and colleagues have extended the basic model to account for the influence of a non-target (distractor) on saccade latency [10].

Here we use a more realistic model system with separate layers for excitatory and inhibitory neurons to explain the interdependency of metrics and timing of visually-guided saccades in double-target paradigms. We focus on tasks where both targets are presented at identical radial eccentricities, the gaze angle, x , being the only free coordinate. The evolution of the activation of neuron x (x corresponds to its spatial location on the motor map) in the excitatory layer, $u(x, t)$, and the inhibitory layer, $v(x, t)$, is governed by the

$$\begin{aligned}
\tau_u \frac{\partial u(x, t)}{\partial t} &= -u(x, t) + \int w_u(x - x') f(u(x', t)) dx' - v(t) + \dots \\
&\quad + S_l(x) + S_r(x) - h_{\text{fix}}(t), \\
\tau_v \frac{\partial v(t)}{\partial t} &= -v(t) + \int w_v f(u(x', t)) dx'.
\end{aligned}$$

τ_u and τ_v are the time constants of the dynamics, $f(u)$ is a nonlinear transfer function, $h_{\text{fix}}(t)$ describes a global time dependent inhibition, $S_l(x)$ and $S_r(x)$ are constant afferent stimuli of Gaussian shape. The excitatory interaction kernel, $w_u(x - x')$, is chosen as a Gaussian, whereas the inhibitory kernel is chosen as constant, w_v , for simplicity.

Our model incorporates characteristics of three important classes of collicular neurons: *build-up neurons*, *burst neurons*, and *fixation neurons* [8]. It is assumed that the activity of build-up neurons continuously increases after presentation of the saccadic target, but that burst neurons start to fire only after the build-up activity has reached a sufficiently high level. This bimodal distribution of thresholds can be modeled as a weighted average of two sigmoid transfer functions with different slopes [11]. We have used a piecewise linear approximation in our simulations with parts f_1 and f_2 for lower and higher activation levels, respectively (Fig. 1A).

Fixation neurons tonically inhibit the saccadic neurons during visual fixation and continuously reduce their discharge rate during the preparation phase of the saccadic eye movement. The effect of the fixation neurons on the network dynamics is modeled by the global inhibition $h_{\text{fix}}(t)$. The release of inhibition after target presentation leads to an increase in excitatory activation. When the activation crosses θ_{burst} , an active burst develops which is assumed to trigger the onset of the saccade. We have applied a slow and a fast time constant for the adaptation of $h_{\text{fix}}(t)$ representing short- and long-latency eye movements in the range of 100 ms and 300 ms, respectively.

3 Results

3.1 Model dynamics: Accumulation mode and decision mode

We hypothesize that the build-up stage and the burst stage of neural dynamics in the SC constitute two functionally different working modes which we denote as *accumulation mode* and *decision mode*. In our model the dynamics switches from the accumulation mode to the decision mode when the excitatory activation u crosses θ_{burst} .

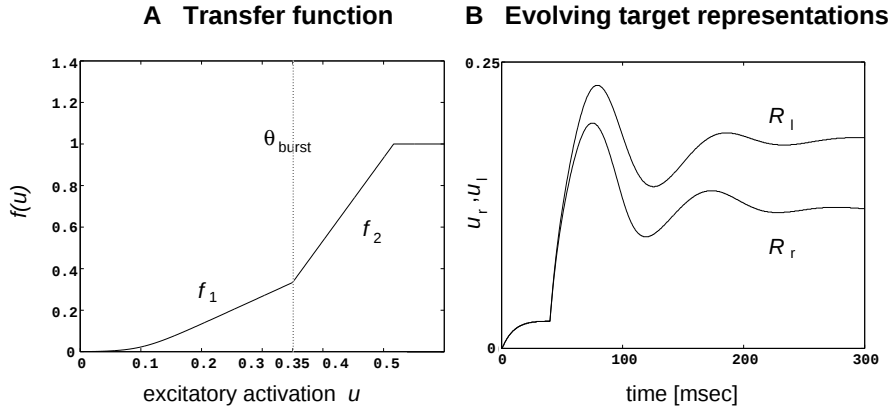


Fig. 1. A) Transfer function. B) Time course of the maximum excitatory activation of the target representations R_l and R_r in the accumulation mode. The global inhibition h_{fix} was not adapted for this simulation example. Two constant stimuli S_l and S_r of slightly different amplitude are applied for $t \geq 40$ ms.

We suggest that the SC temporally integrates visual information about potential targets in the accumulation mode. (1) The visual target stimuli evoke two inputs to the SC which are assumed to differ slightly in their strength due to random fluctuations. The temporal integration then yields two neural target representations on the motor map, the activation levels of which slowly diverge over time. (2) In the short-latency case the activation levels of the target representations are similar at the end of the accumulation phase, but they are clearly distinct in the long-latency case (see Fig. 1B).

In the model the temporal integration of stimuli is the result of an effective time scale which is much longer than the time constants τ_u and τ_v due to recurrent interactions in the network [3].

In the decision mode the activation level is above the burst threshold θ_{burst} (Fig. 2). The steeper slope of part f_2 of the transfer function f guarantees that only a single localized region of activation can persist in this mode.

In the long-latency case, the target representation with highest activation level, R_l , crosses θ_{burst} first and actively suppresses the representation R_r of the second target via strong lateral inhibition (target selection, Fig. 2B).

In the short-latency case, R_l and R_r cross θ_{burst} at about the same time. Since in the two-layer model strong excitation between neighboring field sides starts first and is only followed in time by increasing lateral inhibition, the two target representations merge leading to a localized activity pattern centered between the two target positions (target averaging, Fig. 2A).

3.2 Distributions of saccadic gaze angles

In order to investigate whether our model can qualitatively explain the experimentally observed interdependency of timing and metrics shown in [9], [4] and

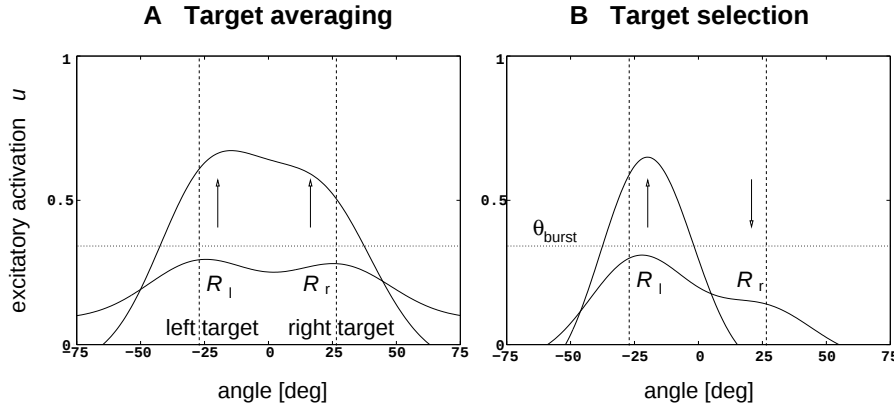


Fig. 2. Evolution of the averaging (A) and selection motor plan (B) in a double-target paradigm.

[2], we generated statistical distributions of saccadic gaze angles for different spatial separations and short- and long-latency saccades. In each of the simulation trials the amplitudes of the stimuli S_l and S_r are drawn independently from a Gaussian distribution. The center of mass of the excitatory activity distribution at the time of maximum activation is chosen as the prepared movement direction for the saccade. The model qualitatively reproduces the main characteristics of the experimental data (Fig. 3): (1) Target averaging at all latencies for closely spaced targets (Fig. 3A). This is due to the fact that the separation of target representations is within the range of mutual excitation during the whole dynamic process. (2) The speed-accuracy tradeoff for intermediate separations (Fig. 3B). The dynamics for this case has been explained in Sect. 3.1. (3) Target selection at all latencies for large separations (Fig. 3C). At short latencies both target representations cross θ_{burst} . However, they cannot merge since at this distance they mutually inhibit each other only.

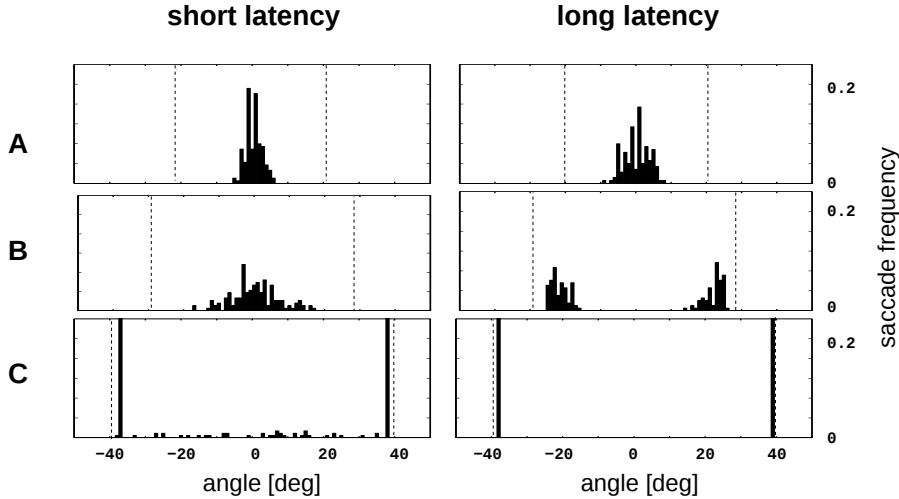


Fig. 3. Distributions of saccadic gaze angles for target separations of 40°, 55° and 80° (A, B and C).

4 Conclusion

Our model reproduces the main characteristic of the behavioral data for the double-target paradigm. This is the dependency of the executed type of saccadic eye movement — averaging or selection — on target separation and saccade latency. We explain these behaviors by two processing mechanisms: accumulation of sensory information and decision making. In conclusion, the modeling results substantiate the supposition that the SC plays a more active role in the preparation of saccadic eye movements than often assumed.

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